Biosystematic studies of species of Delphinium occurring in Montana
by Paul Thompson Sawyer

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree
MASTER OF SCIENCE in Botany
Montana State University

Abstract:
The 11 species of Delphinium occurring' in or expected to be in Montana, Delphinium ajacis, D. andersonii, D. bicolor, D. brownii, D. burkei, D. depauperatum, D. geyeri, D. glaucescens, D. nelsoni, D. nuttallianum and D. occidentale, were studied. Herbarium specimens from Montana State University (Bozeman) and the University of Montana (Missoula) were examined and annotated. The 11 species are grouped into 3 complexes, based upon morphological similarities or dissimilarities. Descriptions and distributions maps of the 11 species are provided, along with a key separating the species.

Delphinium andersonii and D. nelsoni should not be treated as varieties of D. nuttallianum; they are more closely related to D. bicolor than to D. nuttallianum.

Pollen grain and guard cell lengths were determined for 10 species. Pollen grain lengths suggest that D. andersonii might be a polyploid.

Three species, Delphinium bicolor, D. geyeri and D. occidentale, were investigated with serological and electrophoretic techniques. Serological studies did not prove to be reliable or satisfactory. Electrophoretic techniques are useful and could be used in further taxonomic investigations of Delphinium.

BIOSYSTEMATIC STUDIES OF SPECIES OF DELPHINIUM OCCURRING IN MONTANA

by

PAUL THOMPSON SAWYER

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Chairman, Examining Committee

Graduate Dean

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ABSTRACT

The 11 species of Delphinium occurring in or expected to be in Montana, Delphinium ajacis, D. andersonii, D. bicolor, D. brownii, D. burkei, D. depauperatum, D. geyeri, D. glaucescens, D. nelsoni, D. nuttallianum and D. occidentale, were studied. Herbarium specimens from Montana State University (Bozeman) and the University of Montana (Missoula) were examined and annotated. The 11 species are grouped into 3 complexes, based upon morphological similarities or dissimilarities. Descriptions and distributions maps of the 11 species are provided, along with a key separating the species.

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Three species, Delphinium bicolor, D. geyeri and D. occidentale, were investigated with serological and electrophoretic techniques. Serological studies did not prove to be reliable or satisfactory. Electrophoretic techniques are useful and could be used in further taxonomic investigations of Delphinium.

INTRODUCTION

Delphinium L., larkspur, is a large genus distributed principally in the Northern Hemisphere, with many closely-related species in western North America. For economic reasons, *Delphinium* has been and continues to be studied. Several species contain poisonous alkaloids capable of causing death to livestock (Kingsbury, 1964). Certain species are used horticulturally (Bailey, 1949). Therefore, it is important that there be means available for easy recognition of the species and subspecies of *Delphinium*. Such means would, in addition, be of intrinsic value to systematists, as basic information regarding this taxon.

There are 11 species of *Delphinium* present in Montana. There have been no completely satisfactory systematic treatments of the genus in the recent floras of western North America. Using present means, for example, it has been nearly impossible to readily separate *D. bicolor* Nutt., *D. nuttallianum*, Pritz., *D. andersonii* Gray and *D. nelsoni* Greene. It is thought that relatively recent isolation of local populations coupled with a history of interspecific hybridization (Epling and Lewis, 1952) have led to the morphological similarities that make species recognition difficult.

The objectives of this study were:

1. to assign the *Delphinium* specimens of the Montana State University Herbarium to their proper species and
2. to construct a usable key for the identification of taxa of the genus *Delphinium* in Montana.

In addition to morphological studies, certain biochemical systematic methods, phytoserology and electrophoresis, were used to aid in species identification.

REVIEW OF LITERATURE

Taxonomy

The genus Delphinium has been studied by numerous workers. Some of the early workers were De Candolle (1824), Sprengel (1825), Engler and Prantl (1891) and Huth (1892 and 1895). Their work is largely of historical interest and of little value to present day workers dealing with western North American larkspurs as they had but few specimens from isolated parts of western North America to study. Gray (1887) described 5 new species, mostly western North American, of Delphinium including D. andersonii. He failed to give detailed descriptions of these species and his key is confusing, but his study contributes some information towards understanding the Delphinium bicolor, D. andersonii, D. nuttallianum, D. nelsoni complex. Rydberg (1900, 1902 and 1912) described several new species of Delphinium, including D. brownii Rydb. and D. glaucescens Rydb. Currently many of Rydberg's species are thought to represent intraspecific categories rather than specific ranks. Wilde (1931) investigated the larkspurs of horticultural interest. His introduction reviews the status of the genus at the time of his publication.

The most recent comprehensive treatments of western North American species of Delphinium have been those reported by Ewan (1945) in which he investigated all species in North America, and by Hitchcock et al. (1964). Ewan's conclusions are based largely on herbarium specimens, but are secondarily supported by field and plot studies in some cases. He lists 79 species of Delphinium in North America which he places in 13 series designed to show evolutionary lines of development. The Montana species

are placed in the following series:

IV TUBERIFORM SERIES
D. nuttallianum Pritz.
D. depauperatum Nutt.

V LIGNIFASCICULATE SERIES
D. bicolor Nutt.
D. nelsoni Greene

VII ELATOPSOID SERIES
D. glaucescens Rydb.
D. occidentale (Wats.) Wats.
D. brownii Rydb.

XIII SPICIFORM SERIES
D. burkei Greene
D. geyeri Greene
D. andersonii Gray

Ewan states that Delphinium has very few reliable characteristics which can be used to distinguish one species of Delphinium from another. Lewis and Epling (1954) reached a similar conclusion concerning California delphiniums. The most reliable characters are leaf blade appearance, corolla color, petal shape, pubescence of the follicle and seed morphology. Lewis and Epling (1954) caution that herbarium studies without field evidence can cause an investigator to arrive at false conclusions. Lewis (1947) presented evidence that environmental differences can change the expression of the leaf appearance. It has also been noted by Lewis and Epling (1954) that certain field characters such as flower color and sepal form can be obscured or lost in herbarium specimens.

Hitchcock's et al. (1964) study includes the species of Delphinium of northwestern United States and is based on herbarium specimens and field observations. Hitchcock differs from Ewan in interpretation of the

D. bicolor, D. nuttallianum complex. It would appear that D. nelsoni Green, D. bicolor f. helleri (Rydb.) Ewan, and D. bicolor f. macallae Ewan in Ewan's treatment are equivalent to Hitchcock's D. nuttallianum var. nuttallianum. Delphinium nuttallianum var. pilosum C. L. Hitchc. has fibrous roots and is probably the same as Ewan's D. bicolor f. montanense (Rydb.) Ewan. Hitchcock places more emphasis on the deep sinus of the lower petals to separate D. nuttallianum from D. bicolor than does Ewan.

Cytogenetics

The basic chromosome number of Delphinium is 8; the usual diploid number is 16 (Tjebbes, 1928, Mehlquist, Blodgett and Brusica, 1943, Lewis et al., 1951, Lewis and Epling, 1954, Ornduff, 1957, Ewan, 1945 and Hitchcock et al., 1964). Lewis et al. (1951) report 3 exceptions: the 2n number of D. variegatum, D. hanseni and D. gypsophilum being either 16 or 32. The tetraploids appear to be autotetraploids. Chromosome numbers determined for those species present in Montana are D. nelsoni, n=8, (Wiens and Halleck, 1962), D. nuttallianum and D. andersonii, n=8, (Lewis et al., 1951), D. bicolor f. helleri (Rydb.) Ewan, n=8, (Ornduff, 1957) and D. ajacis, n=8, (Tebbes, 1928). Idiograms constructed for several species of Delphinium reveal that the karyotypes are nearly, if not, indistinguishable from one another (Lewis et al., 1951, Mehlquist et al., 1943).

It has been reported by Stone (1961, 1963) and Whitehead (1963) that pollen grain and stomate size are useful in separating diploids and tetraploids of the same genus. However, Lewis and Epling (1954) state

that neither pollen grains or stomate size are useful in separating the diploid and tetraploid races of D. gypsophilum.

Evolution

Ewan (1936) proposed that the genus Delphinium of western North America has undergone prolonged isolation resulting in numerous species which can be grouped into series characterized by similar morphological characters and distribution patterns. Ewan (1945) concluded that one reason closely related Delphinium species were hard to distinguish was due to narrow endemism and highly localized ranges. Epling and Lewis (1952) reached the same conclusions based on field studies carried out over an extended period of time. With respect to the species of Delphinium that they studied, they suggested that:

1. the plants were cross pollinating but self compatible,
2. the plants tolerated severe environmental conditions by remaining dormant over a period lasting up to at least 10 years,
3. individual plants of a colony tolerated different environmental conditions,
4. environmental fluctuations resulted in progeny which were more adapted to that particular type of environmental fluctuation,
5. there was more ecotypic variation at the margins of a colony than at its center, and
6. seed dispersal was probably no greater than 0.2 of a mile.

Lewis and Epling (1952) theorize that the above combination of characteristics is a possible mechanism for separation and isolation of ecotypes

within a colony thus resulting in new colonies, forms or species.

Numerous workers, Mehlquist *et al.* (1943), Ewan (1945), Epling and Lewis (1952) and Hitchcock *et al.* (1964) report that some *Delphinium* spp. hybridize. Epling and Lewis (1952) indicate that hybrids have resulted from interspecific rather than intraspecific hybridization even if diploid and tetraploid members of the same species are present in the same colony. It is thus easy to visualize intergrading variations among species of *Delphinium*.

Hybrids reported to occur in Montana are:

D. bicolor Nutt.	x	*D. nelsoni* Green (Ewan, 1945)
D. andersonii Gray	x	*D. bicolor* Nutt. (Ewan, 1945)
D. burkei Greene	x	*D. bicolor* Nutt. (Ewan, 1945)
	and	
D. andersonii Gray	x	*D. glaucescens* Rydb. (Hitchcock *et al.*, 1964)

Finally, Ewan (1945) suggested that one of the 3 primary distribution centers of *Delphinium* occurs in the Bitter Root Range of the central Rocky Mountains.

Phytoserology

Serological techniques have been used by several investigators to indicate differences between different taxa (Creel 1964, Johnson and Fairbrothers, 1965, Fairbrothers, 1966, and Gell, Hawkes and Wright, 1960, and to identify hybrids (Collins, 1965). Hammond (1955) used serological methods to study generic relationships, including *Delphinium*, in the family Ranunculaceae. Lester, Alston and Turner (1965) used serological techniques to study the genus *Baptisia*. They concluded that serology

couldn't distinguish specific differences within the genus but is useful in defining the genus Baptisia. Since 1960 gel-diffusion techniques (Ouchterlony, 1948 and Creel, Ericson and Schulz-Schaeffer, 1965) have largely replaced the photoreflectrometric method developed by Boyden and DeFalco (1943) in phytoserology.

Electrophoresis

Disc-gel electrophoresis is a new technique developed by Ornstein (1964) and Davis (1964) that can be used to advantage by the biosystematist as pointed out by Boulter, Thurman and Turner (1966). In disc-gel electrophoresis proteins move differentially through the polyacrylamide gel forming bands because of the different electrical charges and molecule sizes of the proteins. The bands formed in the gel at the end of the trial can be compared with bands formed by similar trials using material from other species (Vaughan et al., 1965, and Fox, Thurman and Boulter, 1964).

MATERIALS AND METHODS

Morphological Taxonomy

Nearly 300 herbarium sheets obtained from the herbaria at the University of Montana and Montana State University of *Delphinium* species occurring in Montana were studied. Special attention was paid to those characteristics which appear to be useful in identifying the species. Measurements were made to determine stem height and diameter, lengths of petioles, pedicels, sepal spurs and follicles, and to determine the dimensions of the leaf blades, ultimate leaf segments, flowers, sepals and petals. The stems, leaves and inflorescences were observed under magnification to note the types of surface coverings. Particular note and measurements were made of the extent of notching of the lower petal lobes.

Pollen Grain and Guard Cell Size Studies

The sizes of pollen grains and guard cells from each species of *Delphinium* expected to be found in Montana were measured. Pollen grains were obtained from flowers of herbarium specimens of *Delphinium ajacis*, *D. andersonii*, *D. bicolor*, *D. burkei*, *D. depauperatum*, *D. glaucescens*, *D. geyeri*, *D. nelsoni*, 2 forms of *D. nuttallianum* and *D. occidentale*. The pollen grains were mounted on micro slides in water just before they were to be measured. The long axis of the pollen grain was measured using a calibrated ocular micrometer at a magnification of 500 diameters. Ten pollen grains were measured for each sample. Pollen grains from 10 plants of each species were measured except for 4 species. There were 8 replications of *D. burkei*, 7 replications of *D. depauperatum* and

D. geyeri and 6 replications of D. ajacis.

The data were analyzed statistically using the completely random design, one way classification, analysis of variance with unequal replications (Steel and Torrie, 1960). Duncan's New Multiple Range Test (Steel and Torrie, 1960) having 7 replications was used to determine which of the 11 species differed. Another method used to determine which of the 11 species differed was that of computing 95 per cent confidence intervals for the means of each species using Student's t (Steel and Torrie, 1960).

The guard cell sizes for the same 10 species of Delphinium measured in the pollen grain size study were determined. Dried leaves of herbarium specimens were soaked in water and detergent for 15 minutes and the lower epidermis was then peeled from the leaf and mounted in water on a micro slide. The long axis of the longer guard cell of each stomate was measured using a calibrated ocular micrometer at a magnification of 430 diameters. Ten measurements were made from each leaf. One leaf from each of 6 plants of each species was used for measurements.

The same statistical methods used in analyzing the pollen grain data were used to analyze the guard cell data except there was an equal number of replications, 6, in the analysis of variance.

Serological Studies

Mature leaves from many flowering Delphinium sp. plants were picked in the field. As soon as possible the leaves were brought to the laboratory and washed in running tap water for at least 1 hour. The petioles were clipped from the blades and the blades were blotted dry. The leaves were squeezed using a Carver Extractor (Creel, 1964). About 6 ml of

extracted crude sap was placed in vials and frozen at -20 C immediately after extraction. Caution was taken to exclude from squeezing dried leaves or leaves appearing to be diseased. In the first trial, sap from D. bicolor, D. andersonii and D. occidentale was obtained. Sap from 2 populations each of D. bicolor and D. occidentale and from 1 population of D. geyeri was obtained for the second trial.

Purification of the crude sap for injection into rabbits, injection schedules, bleeding methods and gel-diffusion techniques followed the procedures described by Creel (1964) and Creel et al. (1965) for the first trial. One rabbit was used for each antiserum. Antisera were built for D. bicolor, D. andersonii and D. occidentale.

For the second trial crude sap to be used as antigen material was purified using ammonium sulfate saturation procedures (Colowick and Kaplan, 1955). The crude extract was thawed and centrifuged for 10 minutes at 20,000 xg. 0.243 g of ammonium sulfate and 0.1 ml of 1 per cent protamine sulfate for each ml of supernatant were added to the supernatant. This procedure was carried out in a cold room at about 2 C. After 1/2 hour of stirring in the cold room the suspension was again centrifuged at 10,000 xg for 5 minutes. This time the precipitate was taken up in 2 ml of 2.5 per cent sodium chloride solution buffered at pH 7.0. The buffer contained 0.19 g of monobasic potassium phosphate and 0.75 g of dibasic sodium phosphate with enough water added to make 1 liter of buffer (Johnson and Fairbrothers, 1965). This suspension was dialized overnight in the cold room against the phosphate buffer previously described. The partly purified protein solution consisted of protein

insoluble between the 40-60 per cent saturation point of ammonium sulfate. After dialysing, the amount of protein in the solution was determined using the technique of Lowry et al. (1951). The remainder of the solution was diluted with the buffer so that it contained 1 mg of protein per ml of solution. This material was injected into the rabbit as the antigen source. Antisera were built against antigens from Delphinium bicolor, D. geyeri and D. occidentale using 1 rabbit for each antiserum. The rabbits were injected with 1 mg of protein plus an equal volume of Freund's Complete Adjuvant, subcutaneously in the left and right lumbar regions and in back of the front shoulders. At each injection equal amounts of material were injected into each of the locations. Injections were given weekly for 5 weeks. Two weeks after the last injection the rabbits were bled totally by heart puncture.

Serological tests were made using the modified Ouchterlony techniques of Creel (1964) and Creel et al. (1965). Petri dishes were dipped in a 1 per cent (w/v) solution of Formvar in chloroform. Six ml of 1 per cent # 2 ionager were pipetted into petri dishes 5 cm in diameter. After standing several hours, wells were cut in the gel using a cork borer and a template designed after a pattern used by Johnson and Fairbrothers (1965). The pattern consists of a center well for the antiserum and 4 antigen wells spaced equally apart and 5 mm from the periphery of the antiserum well. All wells are 5 mm in diameter. The antigen was prepared by centrifuging the thawed crude sap for 10 minutes at 20,000 xg. The wells were filled with the appropriate antigen and antiserum using micropipettes and allowed to stand at room temperature for 48 hours. Afterward the serological

plates were washed in water and 0.9 per cent saline solution and the gels were placed on glass slides. The gels were then dried at room temperature and stained with a 0.5 per cent solution of amino schwartz. (Jutila, 1966).

Electrophoresis Studies

Amonium sulfate precipitated proteins from leaf extracts of Delphinium bicolor, D. geyeri and D. occidentale were compared by the use of electrophoresis. The leaf extracts were purified by the techniques described in the second trial of the serological methods section. Lowry's technique (Lowry et al., 1951) was used to determine the amount of protein in the solution. The disc-gels were prepared according to the directions of Davis (1964) except the small pore solution was made with 1.52 parts of working solution A, 3.05 parts of working solution C and 0.88 parts of water. The gel had a pH of 8.4. Fifty micrograms of protein were used for each electrophoresis tube. Eight samples, 4 treatments with 2 replications, were electrophoresised 30 minutes at 5 ma per tube. After electrophoresing the gels were stained in 0.5 per cent amino schwarz in 9:1 methanol, acetic acid for 1 hour and then destained in 7 per cent acetic acid using 8.5 ma per tube for 6 hours. After destaining the banding in the gels was analyzed with a Joyce Chromoscan Densitometer.

RESULTS

Morphological Taxonomy

There are 7 species of Delphinium known to be native in Montana. They are D. andersonii, D. bicolor, D. burkei, D. glaucescens, D. nelsoni, D. nuttallianum and D. occidentale. There are 3 species, D. brownii, D. depauperatum and D. geyeri found in states bordering Montana that may be present in Montana. D. ajacis is a cultivated species existing as an escape in Montana.

Single distinctive characteristics that separate one species of Delphinium from another rarely exist. Those characteristics which are measurable do not usually make suitable key characters because the dimensions of a given character often overlap from species to species. Separation of the Montana delphiniums is based primarily on the root systems, the degree of notching of the lower petal blades, the shapes of the inflorescences, the heights and diameters of the stems, the amounts of leaf blade dissection and the types of stem-coverings.

There are 3 types of root systems. They are the globose cluster typified by D. nuttallianum (Figure 4A and B), the fleshy to tubular fascicle represented by D. bicolor (Figure 3C), and the extensive, woody caudex exemplified by D. andersonii (Figure 2A). The stems of delphiniums are fistulose as in D. occidentale (Figure 1A) or non-fistulose as are those of D. nuttallianum (Figure 4B). The stems can be glabrous, pubescent or glaucous. Some species of Delphinium have spreading hairs, and others have appressed hairs. D. depauperatum has hairs which are basally swollen. The leaf blade may be finely dissected so that the ultimate segments are

numerous and not over 2 mm wide as is illustrated by D. geyeri (Figure 6A). The leaf blade of D. nelsoni (Figure 3A), for example, is several times dissected but not as extensively dissected as the leaf blade of D. geyeri. D. occidentale (Figure 1A) is an example of a species having a cuneate leaf blade with 5-7 broad lobes that are only slightly dissected.

The inflorescence is primarily one of 2 types. It can be spikelike with the flowers borne tight to the rachis so that the inflorescence is about the same diameter throughout its entire length (Figure 1A) as illustrated by D. occidentale. The other type of inflorescence is typified by D. bicolor (Figure 3C). The flowers are borne on spreading pedicels with the pedicels at the bottom of the inflorescence being longer and more spreading than those at the tip of the inflorescence. The notching at the tip of the lower petal can be 1/4 to 1/2 the length of the blade (Figure 3B) or very shallow to erose (Figure 3D).

Table I gives a summary of the characters measured. The key and the species descriptions indicate the final results of the morphological study. Dots on the maps indicate those counties of Montana which have Delphinium specimens represented in the herbaria at the University of Montana or Montana State University.

Table I Measurements from herbarium specimens of various characters of Delphinium species occurring or expected to occur in Montana.

	Stem height	Lower petiole length	Flower number	Flower length	Lower pedicel length	Sepal spur length	Lower sepal length	Notch length	Follicle length	Seed length
	cm	cm		mm	mm	mm	mm	mm	mm	mm
D. occidentale	100-300	4-20	20-90	< 25	< 15	10	10-15	< 2	12-20	1.5-3.0
D. brownii										
D. glaucescens	20-90	10-20	15-50	<25	10-15	8-12	12	0-3	15	1.5
D. geyeri	25-70	6-12	10-30	< 25	10-20	10-15	10-15	0-3	15	2.0-3.5
D. andersonii	25-60	6-15	10-30	20-30	20-30	15-20	10-15	2-4	14-25	2.5
D. bicolor	10-50	2-10	5-20	20-30	10-80	15-20	12-17	< 2	10-17	2.0-2.5
D. nelsoni	15-30	2-10	5-20	20-30	10-40	12-20	12-17	> 2	10-15	2.0-2.5
D. nuttallianum	10-50	2-12	1-8	<30	5-40	10-25	8-15	> 2	10-15	1.0-1.5
D. depauperatum	15-75	3-10	2-15	<30	< 15	8-15	9-15	2	15-20	2.0-2.5
D. burkei	25-70	4-10	10-20	< 25	< 10	10-15	8-12	3	10-15	1.5

Key to the species of *Delphinium* in Montana

A Plants annual; 1-carpellate. — *D. ajacis*

A Plants perennial; 3-carpellate.

B Inflorescence spikelike, appearing as an elongate narrow (usually less than 4 cm wide) cylinder; sepals cupped, not flaring.

C Plants mostly over 1 m tall; major segments of all leaves cuneate.

D Follicles pubescent over entire exposed surfaces. — *D. occidentale*

D Follicles pubescent only along the sutures; rare, if occurring at all in Montana. — *D. brownii*

@ Plants less than 1 m tall; only the major segments of the basal leaves, if any, cuneate.

E Leaves all of one form (finely dissected); stem glaucous, somewhat fistulose and often reddish; flower color dull; root system topped by a woody caudex. — *D. glaucescens*

E Leaves dimorphic, the lower leaves with broad cuneate segments, the upper leaves finely dissected; stems rarely glaucous, fistulose or reddish; flowers bright; roots forming a small fleshy cluster; rare in Montana. — *D. burkei*

B Inflorescence not as above but open, often being wider at the base than the top, often over 4 cm wide; sepals usually flaring but if cupped the root system is not extensive.

F Plants densely pubescent, having a grayish cast; roots and extensive, woody caudex; the ultimate leaf segments not over 1 mm wide; rare, if occurring at all, in Montana. — *D. geyeri*

F Plants not grayish but if densely pubescent the root system is not extensive; ultimate leaf segments over 1 mm wide.

G Plants with a root system topped with a woody caudex; leaf blades all displayed at about the same height; lower petals notched over 1/3 of their length. D. andersonii

G Plants without a woody caudex; leaf blades spaced at different heights on the stem; if the root system is somewhat extensive the lower petals will be notched less than 1/4 of their length.

H Root system forming a globose cluster; sepal spur nearly straight and slender.

I Sepals cupped; inflorescence somewhat spikelike; stem hairs spreading; rare in Montana. D. depauperatum

I Sepals flaring; inflorescence not spikelike; stem hairs appressed downward. D. nuttallianum

J Stems weak, often procumbent; growing in moist alpine environments. High Mountain Form

J Stems sturdy, upright; growing in dry environments Low Land Form

H Root system fibrous or fleshy; sepal spurs curved and stout.

K Lower petals notched less than 1/4 the length of the blade; stem hairs spreading at right angles to the stem. D. bicolor

K Lower petals notched over 1/4 the length of the blade; stem hairs spreading to appressed. D. nelsoni